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One world, many pathogens!

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Commentary

One world, many pathogens!

Forest insect and pathogen species are expanding their geographical ranges through international trade at a rate that most pest specialists and ecologists find alarming. While many invaders are relatively innocuous, several species have damaging impacts on agricultural and natural resources. Furthermore, some of these non-native pests have had catastrophic impacts on ecosystem functions when they invade native communities in which they have no prior evolutionary history. Examples include the demise of chestnut trees in North America, major losses of elms in Europe and North America, Jarrah dieback in Australia, and the devastating effects of pine wood nematode in Asia. Predicting which insects or pathogens will become most problematic and devising mitigation measures to reduce the risk of their arrival and establishment has become the 'holy grail' for many entomologists and plant pathologists worldwide. Analysis of historical data is an essential tool for identifying important invasion pathways and weak links in the chain of biosecurity measures that must be strengthened to protect local economies and ecosystem stability. In this issue of *New Phytologist*, Santini *et al.* (pp. 238–250), provide a comprehensive and insightful analysis of historical forest pathogen establishment and spread records from Europe. A product of a collaborative (20 nations) European Union-funded project, the paper identifies dominant plant pathogen invasion pathways and key factors predicting pathogen species invasiveness, as well as habitat characteristics that render certain regions more vulnerable to pathogen invasion. All of these associations have implications for preventing future invasions.

'…why are there so many more non-native pathogens in Europe than in the United States?'

In their paper, Santini *et al.* observed dramatic changes over time in the sources of forest pathogens establishing in Europe. The earliest known pathogen species establishments were largely a result of intra-European spread. North American species first trickled in during the late nineteenth century, and became even more important during the twentieth century. More recently, Asia has become a major source of pathogens. These changes reflect Europe's expanding sphere of trading partners, particularly for live plant imports, the primary invasion pathway identified in this work and others (Kenis *et al.*, 2007; Liebhold *et al.*, 2012). These observations also suggest a potential 'invasive species source depletion' in which a long history of trade with a given source country results in early establishment of many species followed by fewer invasions as the stock of aggressive invaders becomes depleted. However, the authors correctly observe that there is danger associated with new intra-European invasions originating from previously trade-isolated member states, particularly given the lack of trade barriers currently in place within the European Union.

A surprising wealth of exotic pathogen species established in Europe is documented, compared with recent reports from the United States. Aukema *et al.* (2010) reported only 17 non-native forest tree pathogens established in the United States, whereas Santini *et al.* found 60 in Europe (only 60 of the 91 pathogens alien to Europe infect forest trees, a criterion used by Aukema *et al.*, 2010). This discrepancy suggests that either taxonomists are more diligent at describing new pathogens in Europe, or perhaps Europe's long history of colonialism and more extensive planting of non-native trees may contribute to a heavier burden of introduced pathogens in Europe.

By contrast, Marini *et al.* (2012) reported only 20 exotic Scolytinae (true bark beetles) in Europe vs 58 established in the United States. Indeed, it has been noted that for all groups of forest insects, there is a similar severe but inverse imbalance, with greater numbers of European insect species invading North America than American species invading Europe (Mattson *et al.*, 2007). These authors hypothesized that this imbalance resulted from repeated glacially driven European range expansions and contractions during the Pleistocene and Holocene epochs having resulted in the evolution of competition-hardened species with greater potential as invaders. Santini *et al.* found geographical clumping in vulnerability of countries to invasion that might relate to patterns of climate and biodiversity and may support this hypothesis. But if so, why are there so many more non-native pathogens in Europe than in the United States?

Most forest pathogens are fungi and a steady increase in numbers of emerging fungal plant pathogens worldwide over the last 100 yr has been recently noted (Fisher *et al.*, 2012). It appears that the biology of fungal pathogens somehow causes them to be highly prone to global transport associated with increasing globalization. Novel associations of fungal species with hosts have frequently resulted in the expression of explosive disease epidemics. Furthermore, different fungal pathogen species originating from geographically disjunct locations, when co-locating for the first time, are often capable of hybridizing and producing new pathogens with greater virulence or a different host range than either parent strain (Brasier, 2001; Érsek & Nagy, 2008). Science is just beginning to appreciate the plasticity of fungi, and this plasticity allows them to adapt

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readily to new hosts and habitats. It seems likely that these characteristics of fungal plant pathogens and their close linkages to emerging invasion pathways may explain, in part, the plethora of fungal pathogens responsible for many emerging diseases. In their analysis, Santini *et al.* associate a tendency of pathogens to spread aggressively with a broad host range, particularly if the pathogen is able to attack both forest and ornamental hosts. They also note that pathogens originating from America or Asia spread more aggressively than those originating in Europe or Africa.

These overview analyses of emerging forest diseases in Europe by Santini *et al.* as well as similar analyses of forest insect and disease invasions in other parts of the world (Roques *et al.*, 2009; Aukema *et al.*, 2010; Marini *et al.*, 2012) provide useful characterization of invasion pathways. This information is critical for informing policies on trade and international quarantines. In particular, all of these recent analyses indicate that most forest insect pests and diseases have arrived through one of two pathways: wood products and packaging, and live plant imports. The International Plant Protection Convention (IPPC), in acknowledgment of the importance of these dangerous pathways, has enacted two International Standards for Phytosanitary Measures (ISPMs) to help countries mitigate the risk of future invasions. The adoption of ISPM-15 in 2005 recommends that nations require fumigation or heat-treatment of all wood packing material. Harmonization of national regulations to this standard will facilitate trade and help limit new invasions by wood boring insects as well as some pathogens. Historical evidence indicates that the importation of live plants has facilitated the majority of forest insect and pathogen invasions and unfortunately, there is a strong trend of increasing trade in live plants (Liebhold *et al.*, 2012). This trend could greatly aggravate the forest insect and disease invasion problem. In 2012, the IPPC adopted ISPM-36, which recommends the use of integrated measures at facilities that produce live plants for overseas distribution. Many of the details of how this new ISPM will be implemented and enforced are still being developed. Evidence such as that provided by Santini *et al.* emphasizes the importance of these types of recent efforts to stem the tide of destructive forest insects and pathogens arriving through these pathways.

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